[Plant Signaling & Behavior 1:4, 169-178, July/August 2006]; ©2006 Landes Bioscience

Review

Plant Communication from Biosemiotic Perspective

Differences in Abiotic and Biotic Signal Perception Determine Content Arrangement of Response Behavior. Context Determines Meaning of Meta-, Inter- and Intra-organismic Plant Signaling

Günther Witzany

Correspondence to: Günther Witzany; Telos; Philosophische Praxis; Vogelsangstr. 18c; A-5111-Bürmoos/Salzburg, Austria; Tel.: +43.6274.6805; Fax: +43.6274.6805; Email: witzany@sbg.at

Received 12/06/05; Accepted 06/19/06

Previously published online as a *Plant Signaling & Behavior* E-publication: http://www.landesbioscience.com/journals/psb/abstract.php?id=3163

KEY WORDS

multilevel plant communication, sign-mediated interactions, context-dependency

ACKNOWLEDGEMENTS

I thank Frantisek Baluska for inspiring discussions and Peter Barlow for helpful comments.

NOTE

Biosemiotics (bio = life, Semeion (Greek) = sign). For more information, see page 176.

ABSTRACT

As in all organisms, the evolution, development and growth of plants depends on the success of complex communication processes. These communication processes are primarily sign mediated interactions and not simply an exchange of information. They involve active coordination and active organization—conveyed by signs. A wide range of chemical substances and physical influences serve as signs.

Different abiotic or biotic influences require different behaviors. Depending on the behavior, the core set of signs common to species, families, genera and organismic kingdoms is variously produced, combined and transported. This allows entirely different communication processes to be carried out with the same types of chemical molecules.

Almost without exception, plant communication are parallel processes on multiple levels, (A) between plants and microorganisms, fungi, insects and other animals, (B) between different plant species as well as between members of the same plant species; (C), between cells and in cells of the plant organism.

INTRODUCTION

Based on their apparently static life form, plants have been traditionally been viewed and treated as growth automatons. Today, however, we recognize that the coordination of growth and development in plants, like in all other organismic kingdoms, is possible only by using signs (Greek: semeion) rather than pure mechanics. Understanding the use of signs in communication processes requires a differentiated perspective. Chemical molecules are used as signs. They function as signals, messenger substances, information carriers and memory medium in either solid, liquid or gaseous form.

In this review I will demonstrate that plants are sessile, highly sensitive organisms that actively compete for environmental resources both above and below the ground. They assess their surroundings, estimate how much energy they need for particular goals, and then realize the optimum variant. They take measures to control certain environmental resources. They perceive themselves and can distinguish between self and non-self. This capability allows them to protect their territory. They process and evaluate information and then modify their behavior accordingly.

To understand these highly diverse competences we will notice, that this is possible due to parallel communication processes in the plant body (intraorganismic), between the same and different species (interorganismic), and between plants and non plant organisms (metaorganismic). Successful communication processes allow the plants to prosper, unsuccessful ones have negative, potentially lethal repercussions. Intraorganismic communication involves sign mediated interactions in cells (intracellular) and between cells (intercellular). Intercellular communication processes are crucial in coordinating growth and development, shape and dynamics. Such communication must function on both the local level as well as between widely separated plant parts. This allows plants to react in a differentiated manner to its current developmental status and physiological influences.

As we will see, communicative competence refers to chemical and physical communication processes. Chemical communication is either vesicular trafficking or cell-cell communication via the plasmodesmata. Moreover, numerous signal molecules are produced in or controlled by the cell walls. Physical communication takes place through electrical, hydraulic and mechanical signs.

It should be noted that signs, whether abiotic or biotic, are interpreted. This means they must be identified as components of messages that differ from molecules that are not components of messages (noise). The interpreter is always a living individual. The interpretations can either be successful or unsuccessful. Thus, the message is perceived in its correct sense and meaning and a tailored response behavior is generated. Or it is misinterpreted—sense and meaning are perceived in a distorted or deformed manner—and the response behavior fails to appear or is inappropriate.

We will recognize that the use of molecular languages/codes goes beyond information exchange: it produces various active behaviors and interactions. The many types of symbiosis show that behavior towards the symbionts can be mutually benefit and stress-free. Such relationships can change when this balance is lost, for example when one partner is weakened. The interaction level shifts and one partner views the other as a source of stress. In plants, altruistic forms of interactions occur even in the root zone, as do life-and-death defensive battles. In every case, the situational context determines the meaning of the signs.

We will see that sign-mediated interactions within and between organisms are possible due to the fact that living individuals share a core set of signal molecules with members of their own species but also with members of other species, families, genera or organismic kingdoms: these molecules are produced and emitted at specific levels, amounts and rhythms. The relationship between the molecules is governed by specific rules. The molecular syntax[7,8] of molecular languages/codes determines the correct sequence and combination of signal molecules. Disrupting or deforming these syntactic rules can cause incomplete transmission of the message, triggering faulty interpretations and responses in the receiver. A completely different set of rules determines the interaction behavior between organisms, cells and tissues: growth and development are other forms of behavior than defense or sexual reproduction; mutualistic symbioses require pathways that differ from those in commensalism or parasitism. One and the same core set of species specific signal molecules is used in different interactions to produce different pathways. Moreover, one and the same pathway can take on different meanings (semantic functions) in different interactions and trigger different responses by one and the same receiver. A purely syntactic or semantic analysis cannot explain this because it cannot identify the pragmatic rules that determine the concrete interactions. This calls for considering all three levels of semiotic rules, as in any other analysis of sign use in living nature, and it will show the full range of multilevel communicative competences of plants.

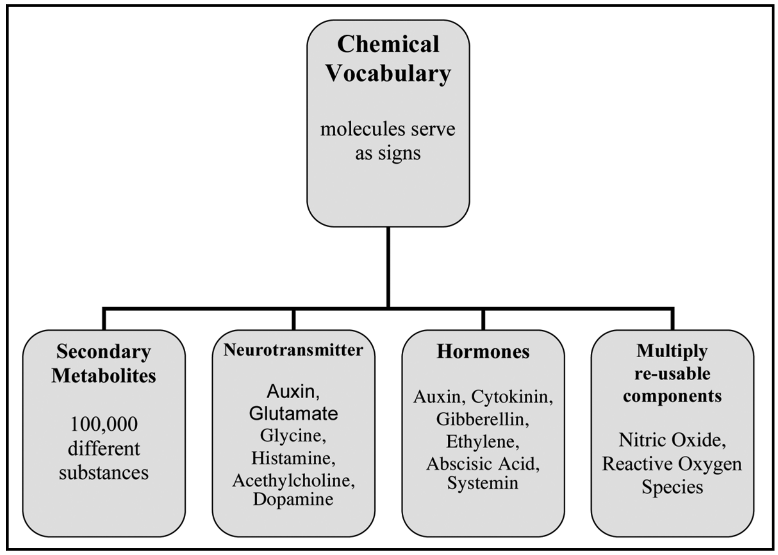

Figure 1. Examples for chemical vocabulary in plant communication processes.

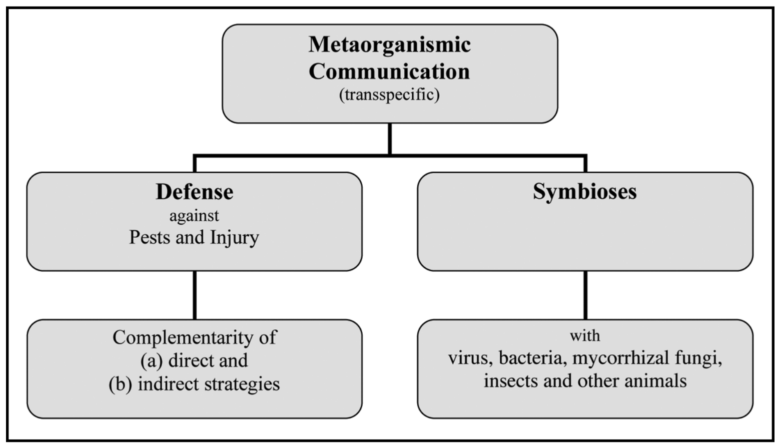

Figure 2. Examples for metaorganismic (transspecies) communication of plants.

CHEMICAL VOCABULARY

The chemical communication in and between plants is so complex that more than 20 different groups of molecules with communicatory function have currently been identified. Up to 100,000 different substances, known as secondary metabolites, are active in the root zone, for example. This diversity is necessary considering the high diversity of microbes, insects and plants in this zone.[9] For example, the continuous defense against pathogenic microorganisms in the root zone requires the constant production, exact dosage and secretion of phytoalexins, defense proteins, and other substances.[10] Here, I present selected examples of the molecular vocabulary in plant communication:

Context-dependent auxin as neurotransmitter, hormone and morphogenic sign. Plant roots and plant shoots detect environmental signals as well as development levels and communicate over long distance pathways. The decentralized nervous system of plants is advantageous for decentral growth and development under constantly changing environmental conditions.[11] Auxin is used in hormonal, morphogenic and transmitter pathways. Because the context of use can be very complex and highly diverse, identifying the momentary usage is extremely difficult.[12] For synaptic neuronal-like cell-cell communication, plants use neurotransmitter-like auxin[13] and presumably also neurotransmitters such as glutamate, glycine, histamine, acetylcholine, dopamine—all of which they also produce.[11] Auxin is detected as an extracellular signal at the plant synapse[12] in order to react to light and gravity. However, it also serves as an extracellular messenger substance to send electrical signals and functions as a synchronization signal for cell division.[14] In intracellular signaling, auxin serves in organogenesis, cell development and differentiation. In the organogenesis of roots, for example, auxin enables cells to determine their position and their identity.[15] The cell wall and the organelles it contains help regulate the signal molecules. Auxin is—as the name suggests—a growth hormone. Intracellularly, it mediates in cell division and cell elongation. At the intercellular, whole plant level, it supports cell division in the cambium, and at the tissue level it promotes the maturation of vascular tissue during embryonic development, organ growth as well as tropic responses and apical dominance.[16]

Hormones. Alongside the classical phytohormones auxin, cytokinin, gibberellin, ethylene and abscisic acid, the plant peptide hormone systemin has noticed to be important; plants use this to systematically react to local injuries.[17] For example, the abiotic stress hormone abscisic acid imparts disease resistance by acting on several levels involved in biotic stress signaling.[18] Peptide signal-mediated responses are merely one part of a biological process that is controlled by a combination of several hormones. In activating an effective defense response, a combination of systemin, jasmonate and ethylene serves as signal molecules.[17]

The production (biosynthesis) of brassinolide hormones is important for cellular processes and development steps. They are therefore termed metahormones.[19] Arabidopsis plants that lack this hormone remain small and are male sterile. Many plant hormones apparently play a key role as signals in cell functions and developments that enormously impact the activities of insects. Plant hormones control not only plant growth and development but also serve in communication within the same species, with related or unrelated plant species, and with insects, i.e. they even serve in classical metaorganismic communication. The fact that plants and insects produce their hormones differently but apply them for similar purposes, namely to coordinate overall development, points to their use in their unicellular ancestors.[20]

RNAs. Sessile organisms can react to the full range of outside influences only through behaviors that are expressed in growth and development; correct timing, which can be very precise, is crucial.[21] Beyond phytohormones, the chemical messenger substances include peptides such as phytosulphokine growth factors and RNAs. Micro-RNAs play an important role in intracellular communication during plant development, either in cleavage during translation/transcription or in preventing translation. Micro-RNAs are apparently necessary for meristem function, organ polarity, vascular development, floral patterning and hormone response. Many of them are developmentally or environmentally regulated.[22] Small interfering RNA probably serves as a signal during early development. In later developmental phases, the RNAi-dependent epigenetic processes are reminded of this early development phase, for example the heterochromatin configuration. At any rate, these RNAs play important roles in chromatin regulation and therefore in epigenetic silencing.[22]

Multiply re-usable components. Small molecules and proteins that normally support important functions in plant immunity, such as nitric oxide and Reactive Oxygen Species (ROS), have now been identified as multiply re-usable components of other biological processes. Messenger substances and signal molecules are used as a versatile basic vocabulary in other contexts and other regulation networks—a common principle in the evolution, growth and development of organisms.[23,24] Nitric oxide (NO) is a substance that has a regulatory function in numerous signal processes such as germination, growth, reproduction and disease resistance.[25] The same is true for diverse species of ROS.[26, 27]

INTERPRETATION OF MECHANICAL INFLUENCES

Mechanical contact has an influence on the overall organism and on the cell level, both in plants and in other eukaryotes. Contact can cause plants (A) to react aggressively, for example toward the animals that want to eat them, (B) to discard their pollen, and (C) can cause the plant stem to grow into the sunlight.[28] The entire configuration of a plant (morphogenesis) is partially determined by mechanical inputs, for example wind and gravity (gravisensing[29]). Responses to contact involve signal molecules and hormones along with intracellular calcium, reactive oxygen species, octadecanoids and ethylenes. Another common feature is contact related gene expression. Many of these genes code for calcium binding proteins, cell wall changes, defense, transcription factors and kinase proteins.[28]

The detection of resources and their periodic, cyclic availability plays a key role in plant memory, planning, growth and development. When, for example, young trees obtain water only once a year, they learn to adjust to this over the following years and concentrate their entire growth and development precisely in the expected period.[30]

Interpretation processes in the plant body are highly sensitive. In taller growing plants, for example, the water balance places enormous demands on cell wall development and cell wall structures, which must adapt to the (often extreme) pressures involved in storage and pressure distribution. A sophisticated and multi leveled feedback- and feedforward-system guarantees a plant compatible water balance even under extreme environmental conditions.[31,32] To date, seven different levels of sensitivity to water shortage have been described. They are based on the different types of physiological and phenotypic responses.[33] Plants are especially sensitive to light and have various receptors for UV, blue, green, red and far-red light.[33] The angle of the light, combined with sensation of the growth of adjoining plants, is decisive in enabling plants to coordinate their growth with respect to the optimal light angle and shade avoidance.[34] The adaptive response of the plant, i.e. altered growth, depends on the seconds-, minutes- and hours-long dominating wavelength of the incoming light, and on the combination of wavelengths across the whole day. The roots receive constant signals from the aboveground parts of the plant for specific growth orientations.[35]

METAORGANISMIC (TRANSSPECIFIC) COMMUNICATION

Sign-mediated interactions with organisms belonging to other species, genera, families and organismic kingdoms are vital for plants and are coordinated and organized in parallel. They are almost always symbiotic or parasitic and range from mutually beneficial via neutral, up to damaging behaviors. The different forms of symbiotic communication require very different behaviors from the participating partners. This involves large numbers of complementary direct and indirect defense behaviors.

Coordination of defense against pests and injury. A good example of parallel meta-, inter- and intraorganismic communication are coordinated defense strategies of plants. Chemical signal substances are the oldest form of signs and are used by microbes, fungi, animals and plants. They are transmitted via liquids in the environment or within the plant body; they can be distributed and perceived through the atmosphere. Leaves always emit such volatiles in small doses, but emit greater quantities when infested by parasitic insects. This allows them to attack the parasites either directly by producing substances that deter them, or indirectly by attracting other insects that are natural enemies of the parasites. These volatiles are also perceived by neighboring plants, allowing them to initiate preemptive defensive responses.[36] Volatile phytochemicals serve as airborne semiochemicals. Depending on the behavioral context—destruction, injury or parasitic infestation—the emitted scents clearly differ for both the insects and neighboring plants.[36] The plants coordinate complementary direct and indirect defense mechanisms in a step-wise manner and tailor them flexibly to the severity of the injury or the density of pest infestation.[37,38]

When plants are attacked by pests, they develop immune responses that function the same as in animals.[39] Injured plants produce aromatic substances that warn other plants. They then rapidly produce enzymes that make the leaves unpalatable for herbivorous insects. Rather than being passive prisoners of their surroundings, plants are active organisms[40] that identify their pests and actively promote the enemies of these pests.[41]

In lima beans, for example, a total of five different defense strategies against mite infestation have been discovered. First, they change their scent to make them unattractive to the mites. Then the plants emit scents that are perceived by other plants, which then do precisely the same thing to warn surrounding lima beans before the mites even reach them. Some of the emitted substances had the effect of attracting other mites that ate the attacking red mites.[42] Similar defense processes have been described in tomato plants.[37,43]

Plants possess a non-self warning system to fend off dangerous parasites. So called pattern recognition receptors detect patterns of chemical substances associated with parasite infestation.[44] The microbes, in turn, react to this pattern recognition.[45]

Because plants are sessile, their reaction potential is geared toward defense against mechanical damage and pest infestation. One of the many reaction types to infestation is the production of protease inhibitors I und II, which block protein degradation in the digestive tracts of insects. This defense reaction is produced both at the injured site and throughout the surrounding tissue: the local wound response triggers the production of mobile signals that prompt a systematic reaction of the overall plant.[17]

Plant roots have the capacity to produce 100,000 different compounds, largely secondary metabolites, many with cytotoxic properties, in order to prevent the spread of microbes, insects and other plants.[9,46] For example, plants have developed defense strategies in which substances are emitted in the root zone such as signal mimics, signal blockers and/or signal degrading enzymes to respond to bacterial quorum sensing.[46] In the defensive position, they can disrupt the communication of parasitic microorganisms to the point that the internal coordination of the parasitic behavior collapses.

Beneficial arthropods such as predaceous or fungivorous mites are supported by plant domatia, similar to the situation in complex communities of grasses and fungal endophytes. These symbiospheres, however, can also be misused, for example by mites that colonize these domatia for themselves without benefiting the host cell.[47]

Communicative coordination of symbioses. A limited number of chemical messenger substances is available to maintain and simultaneously conduct the communication between (A) root cells of three different types, (B) root cells and microorganisms, (C) root cells and fungi and (D) root cells and insects.[9,46,48-51] The communication process in the root zone is generally meta-, inter- and intraorganismic and requires a high communicative competence in order to be successfully interactive on all three levels and to distinguish messenger molecules from molecules not being part of messages.[52-54] It has been postulated that the origin of root cells in plants, and therefore the basis for the youngest organismic kingdom on our planet, arose through the symbiogenesis of fungi and algae.[35,55,56] One hypothesis assumes that land plants are the symbiogenetic product of green algae and a tip-growing fungus-like organism that combined autotrophic and heterotrophic capabilities.[57]

Vital symbiosis of plant roots with bacteria, fungi and insects. Plants use their plant-specific synapses[12] to conduct neuronal-like activities and establish symbiotic relationships with bacteria.[58] Similar mutually advantageous relationships are established with mycorrhizal fungi.[59] A special type of plant synapse resembles the immunological synapse of animal cells and allows plants to respond to pathogen and parasite attacks as well as to establish stable symbiotic

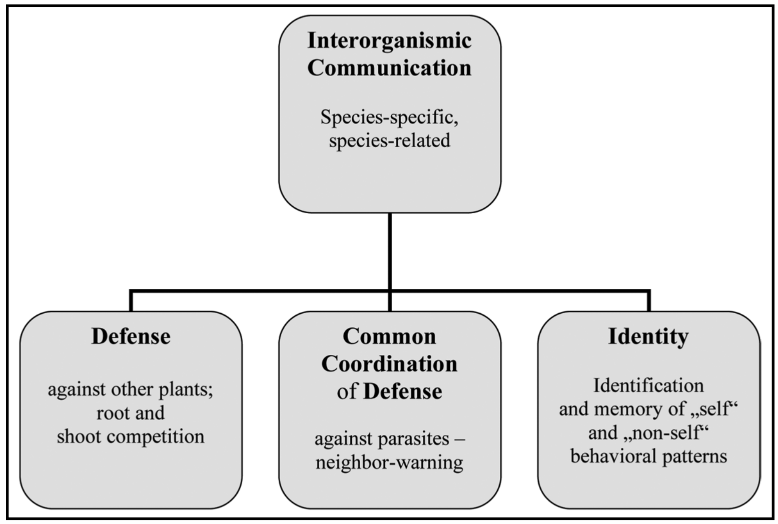

Figure 3. Examples for interorganismic (species-specific, species-related) communication of plants.

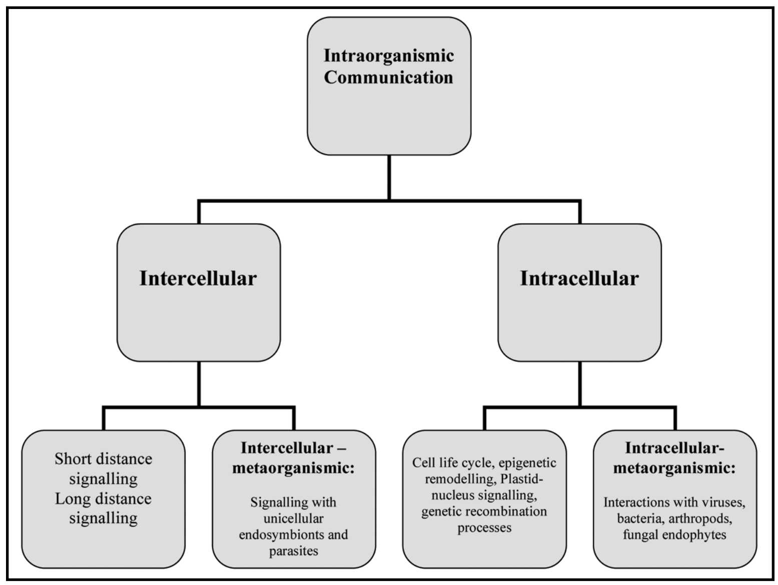

Figure 4. Selected examples for intraorganismic communication of plants.

interactions with rhizobia bacteria and fungal mycorrhiza.[12,60-64] Electrical signals can reinforce chemical signals or overcome short distance responses of fungal mycelia that can be present on root surfaces.[65] Interestingly, rhizobia bacteria are taken up in plant cells via phagocytosis during symbiotic interactions with roots of leguminous plants.[66] The symbiotic relationship between legumes and rhizobial bacteria leads to the formation of nitrogen binding nodules in the root zone. Nod factor signaling and thigmotrophic responses of root hairs overlap here as well. This once again shows how the same pathways are used for different signal processes.[67]

Today, several hundred species of fungi colonize more than 100,000 different plant species. This type of cohabitation requires symbiotic signaling.[68] Roots develop from rhizomes in order to provide better conditions for mycorrhizal fungi, which in turn supply plants with better nutrients.[69] For the fungus the relationship is either balanced or predatory. Endophytic fungi, however, live in plants without triggering disease symptoms.[69] Similar to the symbiosis between plants and mycorrhizal fungi, the symbiosis between asexual endophytes and grasses also represents a type of complementary parasitism.[70]

Plants, insects and microbes share a particular repertoire of signals. Some are therefore also employed strategically. Thus, plants also use insect hormones (prostaglandins) for specific defense behavior. Signal theft is common. Because plants can detect their own signals, they can presumably also detect similar signals that are used in communication between insects.[71]

Viral symbiotic interactions. In particular, the evolution of plant viruses shows that viruses complement plants both competitively and symbiotically. A healthy plant body is better for most viruses than a sick body. Plant viruses and their development provide a good explanation for the observation that new species originate through symbiogenesis.[72] Viruses use intergenomic gene transfer and intragenomic duplication. Many DNA viruses have encoded numerous nucleic acid metabolisms that are very similar to cell proteins. Examples include DNA polymerases, ribonucleotide reductase subunits, DNA dependent RNA polymerase II subunits, DNA topoisomerase II, thymidylate synthase, helicases and exorbinuclease. Viruses probably invented DNA to protect their genetic material from being changed by RNA or RNA encoded enzymes.[73] One of the interaction processes between plant viruses and their host organisms creates a defense level against foreign nucleic acids.[74] Plant viruses code for silencing suppressors in order to act against host RNA silencing, and some of these suppressors effect micro-RNA multiplication and hinder plant development.[75] But also viroids play a symbiotic role. Despite their small size and their non-coded genome, viroids can multiply, systematically spread from cell to cell, and trigger symptoms in the host.[76]

INTERORGANISMIC COMMUNICATION

Research has shown that plants can distinguish between damage caused by insects and mechanical injuries. Mechanically injured plants emitted substances that were ignored by neighboring plants, whereas they all reacted immediately to pest infestation.

Plants can distinguish between self and non-self. Thus, defense activities are initiated against foreign roots in order to protect the plant's own root zone against intruders. The individual sphere of a root, along with its symbiotic partners, requires certain fundamental conditions in order to survive and thrive. When these prerequisites are threatened by the roots of other plants, substances are produced and released in the root zone that hinder this advance.[9,46,49,50] Such defense activities are also deployed as anti-microbial substances against the microflora in the root zone.

Plant roots produce a wide range of chemical substances: (A) some enable species specific interactions; (B) many of these substances are released tens of centimeters into the surroundings; (C) these substances have strong but not necessarily negative effects on animals, bacteria, viruses and fungi; (D) released substances have a defensive function against other plants; (E) many substances have absorptive characteristics that reduce the negative effects of substances.[9]

As reported above in lima beans and tomatoes, also corn plants use a sophisticated communication system to warn each other about pests. By emitting green leafy volatiles, the corn plants attract the natural enemies of the pests and alarm neighboring plants. The alarmed neighbor then produces a protective acid that is normally produced only in response to external injuries.[38] Plants use biotic signals to inform each other about the presence, absence and identity of neighboring plants, growth space, growth disturbances and competition.[48] Plants that are removed and planted elsewhere remember the identity of their former closest neighbors for several months.[77] Recognition patterns in neuronal like networks are one possible explanation.

Parasitic plants are an important feature in the plant world. Today, about 4,000 species have been described. In order to parasite other plants, their root apices transform into fungal like haustoria which extract photosynthates from vascular tissue of pray roots.[61,78] Parasitic plants are present wherever other plants can grow, from the tropical rainforest to the Arctic, and take important nutrients and environmental resources (light) away from non parasitic plants. They therefore influence entire ecosystems, population dynamics, and biodiversity, including the presence and diversity of microbes, birds, insects and other animals.[79]

INTRAORGANISMIC COMMUNICATION

As opposed to the central nervous system of animals, which controls metabolism and reactions centrally, the control in plants is decentral.[80] This enables plants to start independent growing or developmental activities in certain regions of their body, for example on how a particular branch should grow, depending on the wind, light angle and overall "architecture" of the plant.[33] Most of the activities that plants make with regard to growth and development require communication processes—synapse-like communication—between all parts of the plant.

Intercellular communication. Short-distance communication differs considerably from long-distance communication. As a rule, both complement each other. Intercellular communication in the root zone (in the soil) differs from that in the stem region above ground. Both are necessarily coordinated with one another in order to enable life in these different habitats. Intercellular communication informs other plant parts about events in specific organs or regions of the plant (especially in large plants), for example sugar production in leaves, the reproduction in flowers and resource utilization by the roots.[81]

Plant cells are connected by plasmodesmata. These connecting channels enable the flow of small molecules as well as ions, metabolites and hormones, and allow the selective exchange (size exclusion limit) of macromolecules such as proteins, RNAs and even cell bodies.[82] The plasmodesmata impart plants with a cytoplasmatic continuum known as the symplasm.[76] But plasmodesmata are more than mere transport channels; they also regulate and control the exchange of messenger substances in a very complex manner.[83] In symplastic signaling, the intercellular communication of plants differs fundamentally from that in other organismic kingdoms.[84] It integrates various communication types such as local and long distance communication. Beyond symplastic communication (especially in the meristem, where new tissues are produced), plants also exhibit the receptor-ligand communication typical of animals.[84] While receptor ligand communication determines stomatal patterning in the epidermis of mature leaves, trichome patterning is mediated by symplastic signaling.[85]

For long-distance signaling movement proteins play an important role. Movement proteins convey information bearing RNA from the stem and leaves to the remote roots and flowers. The movement protein allows the mRNA to enter the plasmodesmata tunnel, into the phloem flow. Once it has entered this transport system, it can relatively rapidly reach all parts of the plant. These RNAs can control the levels of other proteins. The level contains information for local tissues, for example about the general physical condition of the plant, the season, or the presence of dangerous enemies.[81]

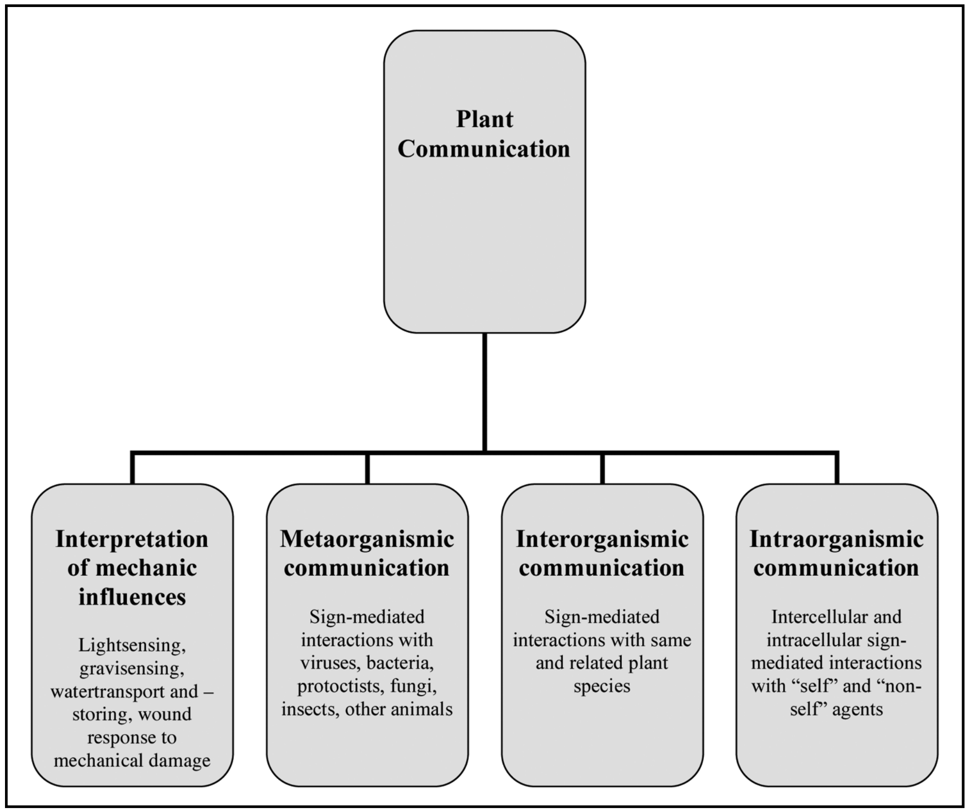

Figure 5. Plant communication processes are sign-mediated interactions which each obey three levels of semiotic rules (syntactic, pragmatic, semantic).

Plasmodesmata are prerequisites for intercellular communication in higher plants.[86] In embryogenesis they are an important information channel between fetal and maternal tissue. The further the development of the embryo, the more reduced the cell-cell communication between embryo and maternal tissue.[87] Cell-cell communication via direct transmission of transcription factors plays a central role in root radial and epidermal cell patterning as well as in shoot organogenesis.[88] The cellular organization of the roots is determined during the plant's embryonic development and is controlled by intercellular communication. Bonke et al.[89] provide a particularly good example of communicative control of these ten phases of embryogenesis. This confirms the presence of local signaling centers and the complex relationship between numerous different signaling pathways.

A wounded plant organizes an integrated molecular, biochemical and cell biological response. This strategy enables information to be transported across great distances, for example in tall trees.[90] Proteins that can be detected by receptors enable a socalled thoughtful response[91] by plants. There are about one thousand known protein kinases/phosphatases, numerous secondary messengers and many thousands of other proteins.[33] Through their life cycles and their growth zones, plants develop a life history of environmental experience that they can pass on to later generations and, should they themselves grow to be several hundred years old, utilize themselves.[33] Even small plants store stress experiences in their memories and then use these memories to coordinate future activities.[92] Especially during growth, key information about the current status often takes a back seat to future oriented processes, for example early root growth and nutrient supply to secure future developments such as larger leaves. From this perspective, plants must plan for the future and coordinate growth, food uptake and communication with symbionts.[93]

The complementary differentiation of communication types into short-distance and long-distance signaling—with their different yet ultimately complementary tasks—requires cells to identify their position. They accomplish this by, among other things, detecting signals from neighboring cells.[94] Thus, the identification competence of self and non-self by cells can be interpreted as a result of social interaction rather than solipsistic behavior. For example, signals from leaves trigger flower development at the tip of a plant.[94] An entire network involving four different signal pathways regulates this transition from the vegetative to the reproductive phase.[94] Most flowers bear closely adjoining male and female reproductive organs. Self-incompatibility is therefore crucial in distinguishing between own (related) and foreign (non-related) pollen. This self/non-self differentiation ability is promoted by signal processes also used in other plant responses.[95]

Signals amend one another to form signal sequences, much like words combine to form sentences: different active forms of behavior determine the combination and production through molecule-sequences. This distinguishes cell differentiation during root development from cell differentiation during stem development, or developmental processes during the vegetative phase from developmental processes in the reproductive phase.

Intracellular communication. Intracellular communication in plants takes place between the symbiogenetically assimilated unicellular ancestors of the eukaryotic cell, mainly between the cell body and cell periphery. It transforms and transmits external messages into internal messages that exert a direct (epigenetic) influence on the

DNA storage medium and trigger genetic processes; this leads to the production of signal molecules that generate a response behavior. Via endocytosis, however, bacteria, viruses and viroids interfere with this intracellular communication and can support, disrupt or even destroy it. Intracellular communication offers viruses the opportunity to integrate certain genetically coded abilities of the host into their own genome or to integrate their own genetic datasets into the host genome. The ability of viruses to integrate different genetic datasets probably plays a major role in symbiogenetic processes. The eukaryotic cell is composed of a multicompetent nucleus as a basic building block of life and a cell periphery-apparatus that was symbiogenetically the ancestor of other endosymbionts. Interestingly, both the nucleus and viruses have several similar features and capabilities: they both lack the protein synthesis pathways and the fatty acid producing pathways. Both transcribe DNA but do not translate it into RNA. Viruses were probably very important in the evolution of eukaryotic cells because they were able to conduct cell-cell union.[96] There are strong reasons too, that the eukaryotic nucleus is of viral origin.[97-99]

Neuronal plasticity refers to the ability of neuron populations to alter—to either strengthen or weaken—their connections based on experience. This is the basis for learning and memory. Like memory, long-term neuronal plasticity requires new RNA and protein synthesis. Accordingly, the signals must be transported from the synapse, from where they are sent, to the nucleus, where they are transformed to change the gene transcription. Then, the products of gene transcription (proteins, RNAs) must be sent back to the synapse in order to permanently change synaptic strength. This communication process is well described in animals;[100-102] if plants exhibit neuronal plasticity, then similar descriptions may follow.

Reports on the transfer of mitochondrial genes between unrelated plant species caused some surprise. While gene transfer is an extremely rare event in animals and fungi, it is common between plant mitochondria.[103] Variations in repetitive DNA that manifest themselves as variation in the nuclear DNA complex have far-reaching ecological and life history consequences for plants.[104]

The function of a eukaryotic cell depends on successful communication between its various parts. Plastids send signals to regulate nuclear gene expression and thus to reorganize macromolecules in response to environmental influences.[105] It has been shown that micro-RNAs regulate certain developmental processes such as organ separation, polarity and identity, and that they define their own biogenesis and function.[106] Eukaryotic genomes are regionally divided into transcriptionally active euchromatin and transcriptionally inactive heterochromatin.[107] Epigenetic changes can also take place without changes in genomes, for example through various inactivations and activations of genetic datasets via chromatin remodeling, transposon/retro release, DNA methylation, novel transcription, histone modification, and transcription factor interactions.[108] Epigenetic changes are also reversible.[109] Various stress situations in plants are known to cause transposon movements,[110] and bacterial infections or UV stress can cause chromosomal rearrangements,[111] i.e. changes in higher-order regulation levels that control the transcription processes of the protein-coding DNA.

Repetitive DNA is present in two syntactic combinations: tandem repeats and dispersed repeats. Tandem repeats consist of sequences that can contain several thousand copies of elements that are dispersed throughout the genome. Pericentromeric sequences consist of a central repetitive nucleus flanked by moderately repetitive DNA. Telomeric and subtelomeric sequences consist of tandem repeats at the physical end of the chromosomes. Retroelements and transposable elements are involved in replication and reinsertion at various sites in complex processes: these include activation of excision, DNA-dependent RNA transcription, translation of RNA into functioning proteins, RNA-dependent DNA synthesis (reverse transcription) and reintegration of newly produced retroelement copies into the genome.[104]

Endocytosis and vesicle recycling via secretory endosomes are indispensable for many processes in multicellular organisms. Plant endocytosis and endosomes are important for auxin mediated cell-cell communication as well as for gravitropic responses, stomatal movements, cytokinesis and cell wall morphogenesis.[112] As in animals, synaptic cell-cell communication is based on rapid endocytosis and vesicular recycling in plants.[12]

Plants can overwrite the genetic code they inherited from their parents and revert to that of their grand- or great-grandparents.[113-115] This contradicts traditional DNA-textbook conviction that children simply receive combinations of the genes carried by their parents. Now a backup code has been found; it can bypass unhealthy sequences inherited from the parents and revert to the healthier sequences borne by their grandparents or great-grandparents. Research has shown that plants are able to replace abnormal parental code sequences with the regular code possessed by earlier generations. Does this require inheritance not only of the parental genetic make-up but also that of the grandparents and former ancestors? What is proposed is that higher-order regulation function in non-coding DNA—a type of genome editing MetaCode[116]—save ancestor genome structures, which overrule protein-coding DNA under certain circumstances like stress. This means that the (pragmatic) situational context of the living plant body may induce epigenetic intervention on the genome editing MetaCode, i.e. active micro-RNAs activate a certain signaling pathway network which can restructure syntax (combination) and semantics (meaning) of a genetic make-up. Initiating chromosomal methylation and histone modifications, certain silencings, start and stops, and alternative splicing processes constitute alternative sequences. The result is that, in the existing genome architecture, not the inherited parental sequences are translated and transcribed but the backup copy of grand- or great-grandparents. Under normal conditions, the operative genetic make-up stems from the parents. These research results indicate that not only is a combination of parental genes inherited, but also ancestral genome regulating features in non-coding DNA; this enables alternative splicing pathways, i.e. a different use and multiple protein meanings of one and the same genetic data set.[113-115]

OUTLOOK

Plants are the youngest organismic kingdom and perhaps the main success story of evolution. They arose ca. 350 million years ago, and terrestrial plants, which flower and bear fruits (a key prerequisite for feeding in larger animals), only developed 150 million years ago. Higher plants make up 99% of the biomass on our planet; of this, nearly 84% are trees. The lack of mobility is often construed as a disadvantage vis à vis representatives of the animal kingdom. From an objective perspective, such immobility and the sessile life style must have been an advantage. Plants are clearly the most malleable of organisms, a trait that can be attributed to the symbiogenetic unification of 5–7 different unicellular, ancestral organisms.

An ever increasing body of data shows that evolution, growth and development—as in all other organismic kingdoms—depends on successful communication processes. This feature is the prerequisite for the internal coordination and organization of the organism and its interplay with other organisms. Communication processes, however, go beyond mere information exchange to include highly differentiated and manifold sign-mediated interactions. The signals used in these interaction processes underly certain semiotic rules. The rule adherence is very reliable and conservative. Nonetheless, the rules governing sign use can be damaged, incompletely executed, deformed, abandoned, or even newly generated. Therefore biosemiotic rules—as opposed to natural laws—are principally changeable.

As in all sign processes (semioses) in living nature, syntactic rules determine the relationship of the signs to one another, i.e. provide combination rules for the sequence, combinatory ability, density and rhythm of the signs used. The syntactic rules differ from pragmatic rules. They enable entirely different interactions in that the interaction partners must generate a very specific behavior in order to interact, for example mutual coordination and organization, to be successful at all. Here, concrete life situations with very specific behavioral contexts are involved. Depending on the context of use, one and the same syntactically correct sign sequence of chemical signal molecules can take on different meanings (semantic functions).

Plants fundamentally depend on successful communication. The behavior in the specific interaction can be misinterpreted. A plant can feign mutualism, for example, in order to gain a one-sided advantage from the interaction and to damage, permanently exploit or kill the partner. This, however, cannot be the representative form of communication because no individuals would survive if all plants behaved in this manner. The majority of interactions must be successful for several participants.

Communication processes are successful when the rules governing sign use are correctly followed. Clearly, rules can be broken. In such cases, the messages transmitted via the signs are incomplete, incorrect, and induce no or a false behavioral response. Messages can also be misinterpreted: The sign user uses (A) the sign incorrectly/misleadingly, and the message does not arrive in the manner intended and for the envisioned purpose because it is mutilated, fragmentary. In a due course, the recipient cannot respond the message in the manner required by the non-mutilated message. (B) The sign continuously expresses a message that does not conform with reality ("insect enemies are attacking"); the recipient of the message will respond in a manner adapted to the reality of this inconformity. (C) The message is used to mean something other than it is normally used to convey (in order to gain one sided advantages). Any constant rule-breaking blocks the organization of life processes (communicative coordination of evolution, reproduction, growth, development) within and between organisms.

The term semiochemicals was generally used to designate molecules or substances (hormones) that served in communication between organisms. As the present review demonstrates all chemicals which function as signs in sign-mediated interactions in and between organisms are semiochemicals. This would be coherent with the biosemiotic approach, which considers the full range of sign use within and between living organisms.[2]

In the future, the meta-, inter- and intraorganismic levels of communication processes will be better understood. This, in turn, will allow better differentiation of the different levels of rules that govern signal use. The syntax of intracellular sign use differs from the syntax at the intercellular level, as well as from the syntax of the signs in species-specific interactions, which in turn differs from sign use in trans-specific interactions between organisms. Embedded in the ecological framework, these rules for constituting sign-mediated interactions are used differently depending on the behavioral context. One and the same message can contain, in other contexts, entirely different meanings. Integrating this biosemiotic perspective will help to more gradually decipher the specific meaning of the full range of semiochemicals (in their broader sense) and to get aware of the high level communicative competences of plants.

Note

Biosemiotics [bio = life, Semeion (Greek) = sign].

Biosemiotics is a transdisciplinary science involving theoretical and empirical studies which investigates sign processes (semioses) within and between organisms in manifold communication patterns. Signs may be signals or symbols, most of them chemical molecules, but also physical ones. In highly developed eukaryotic kingdoms, behavioral patterns of organisms may also serve as signs (signals and/or symbols), as for example, the dances of bees; or these signs may be phonetic, as in songbirds or humans.

The signs used obey semiotic rules of three types in principle. Syntactic rules determine combinatory physical, chemical, spatial, temporal, rhythmical possibilities. Pragmatic rules determine interactional content—e.g., growth, development, defense, mating. And those which are dependent on pragmatic interactional content are the semantic rules, i.e. the meaning function of signs and sign sequences (e.g., in signaling pathways).

Individuals in populations share a common set of signs and a common set of rules. These also apply at the level of cell biology. Dependent on the situational context of interacting entities, signs, or sequences of signs, can have different meanings and functions. Therefore it is possible that different cell types are developed from the same genome trough different chromosomal methylation patterns. Biosemiotics includes not only sign processes used within cells in the context of their molecular and in cell biology, but also embraces immunological, metabolic, neurological and hormonal signalling networks.To many biosemioticians, the origin of life is the starting point of semiosis and vice versa.[1-5]

So far, biosemiotic terms have been used as metaphors in molecular and evolutionary biology, as well as in genetics and ecology, the conviction being that they could ultimately be replaced by chemical and physical descriptions. As a result, the paradigmatic differences between biosemiotic and chemical/ physical descriptions are becoming ever more evident and enable biosemiotics to draw a clear distinction between the biotic and abiotic domains: "Life is distinguished from the nonliving world by its dependence on signs".[6] Thereby, it is possible to use biosemiotics to vastly expand the perspective of biological processes. Consequently, the decisive aspects for life processes are not just with respect to the states of matter and their corresponding changes based on natural laws, but the communication and information processes within and among cells, tissues, organs, organisms. Their importance determines the success or failure to promote life, growth, development, disease and death in all living beings.

References

1. Witzany G. Natur der Sprache—Sprache der Natur. Sprachpragmatische Philosophie der Biologie. Würzburg: Königshausen und Neumann, 1993.
2. Witzany G. The *Logos* of the *Bios* 1. Contributions to the foundation of a three-leveled biosemiotics. Helsinki: Umweb, 2006.
3. Hoffmeyer J. Signs of Meaning in the Universe. Bloomington: Indiana University Press, 1996.
4. Barbieri, M. The Organic Codes. The birth of semantic biology. Ancona: PeQuod, 2001.
5. Markos A. Readers of the Book of Life. Oxford, New York: Oxford University Press, 2002.
6. Pattee HH. The physics and metaphysics of biosemiotics. J Biosem 2005; 1:281-301.

7. Eigen M, Winkler R. Das Spiel—Naturgesetze steuern den Zufall. München: Serie Piper, 1975.
8. Witzany G. From the "logic of the molecular syntax" to molecular pragmatism. Ev Cog 1995; 1:148-68.
9. Bais HP, Park SW, Weir TL, Callaway RM, Vivanco JM. How plants communicate using the underground information superhighway. Trends Plant Sci 2003; 9:26-32.
10. Flores HE, Vivanco JM, Loyola-Vargas VM. 'Radicale' biochemistry: the biology of root specific metabolism. Trends Plant Sci 1999; 4:220-6.
11. Baluska F, Mancuso S, Volkmann D, Barlow P. Root apices as plant command centres: the unique, 'brain like' status of the root apex transition zone. Biologia (Bratisl) 2004; 59:7-19.
12. Baluska F, Volkmann D, Menzel D. Plant synapses: actin based domains for cell to cell communication. Trends Plant Sci 2005; 10:106-11.
13. Schlicht M, Strnad M, Scanlon MJ, Mancuso S, Hochholdinger F, Palme K, Volkmann D, Menzel D, Baluska F. Auxin immunolocalization implicates vesicular neurotransmitter like mode of polar auxin transport in root apices. Plant Sign Beh 2006; 1:122-30.
14. Campanoni P, Blasius B, Nick P. Auxin transport synchronizes the pattern of cell division in a tobacco cell line. Plant Physiol 2003; 133:1251-60.
15. Casson SA, Lindsey K. Genes and signalling in root development. New Phytol 2003; 158:11-38.
16. Friml J, Wisniewska J. Auxin as an intercellular signal. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:1-26.
17. Xia Y. Peptides as signals. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:27-47.
18. Mauch Mani B, Mauch F. The role of abscisic acid in plant pathogen interactions. Curr Opin Plant Biol 2005; 8:409-23.
19. Amzallag GN. Brassinosteroids as metahormones: evidences from specific influence during critical period in Sorghum development. Plant Biol (Stuttg) 2002; 4:656-63.
20. Thummel CS, Chory J. Steroid signaling in plants and insects—common themes different pathways. Genes Dev 2002; 16:3113-29.
21. Fleming AJ. The plant extracellular matrix and signaling. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:85-107.
22. Kidner CA, Martienssen RA. The developmental role of micro RNA in plants. Curr Opin Plant Biol 2005; 8:38-44.
23. Farmer E, Schulze Lefert P. Biotic interactions: From molecular networks to inter-organismal communities. Curr Opin Plant Biol 2005; 8:343-5.
24. Torres MA, Dangl JL. Functions of respiratory burst oxidase in biotic interactions, abiotic stress and development. Curr Opin Plant Biol 2005; 8:397-403.
25. Delledonne M. NO news is good news for plants. Curr Opin Plant Biol 2005; 8:390-6.
26. Apel K, Hirt H. Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 2004; 55:373-99.
27. Carol RJ, Dolan L. The role of reactive oxygen species in cell growth: lessons from root hairs. J Exp Bot 2006; 57:1829-34.
28. Braam J. In touch: plant responses to mechanical stimuli. New Phytol 2005; 165:373-89.
29. Morita MT, Tasaka M. Gravity sensing and signaling. Curr Opin Plant Biol 2004; 7:712-8.
30. Hellmeier H, Erhard M, Schulze ED. Biomass accumulation and water use under arid conditions. In: Bazzaz FA, Grace J. eds. Plant Resource Allocation. London: Academic Press 1997:93-113.
31. Zimmermann u, Schneider H, Wegner LH, Haase A. Water ascent in tall trees: does evolution of land plants rely on a highly metastable state? New Phytol 2004; 162:575-615.
32. Buckley TN. The control of stomata by water balance. New Phytol 2005; 168:275-92.
33. Trewavas A. Green plants as intelligent organisms. Trends Plant Sci 2005; 10(9):413-9.
34. Ballare CL. Keeping up with the neighbours: phytochrome sensing and other signaling mechanisms. Trends Plant Sci 1999; 4:97-102.
35. Baluska F, Volkmann D, Hlavacka A, Mancuso S, Barlow PW. Neurobiological view of plants and their body plan. In: Baluska F, Mancuso S, Volkmann D. eds. Communication in plants. Berlin/Heidelberg: Springer, 2006:19-35.
36. Pare PW, Tumlinson JH. Plant volatiles as a defense against insect herbivores. Plant Physiol 1999; 121:325-31.
37. Kant MR, Ament K, Sabelis MW, Haring MA, Schuurink RC. Differential timing of spider mite induced direct and indirect defenses in tomato plants. Plant Physiol 2004; 135:483-95.
38. Engelberth, J, Alborn HT, Schmelz EY, Tumlinson JH. Airborne signals prime plants against insect herbivore attack. Proc Natl Acad Sci USA 2004; 101:1781-5.
39. Nürnberger T, Brunner F, Kemmerling B, Piater L. Innate immunity in plants and animals: striking similarities and obvious differences. Immunol Rev2004; 198:249-66.
40. Peak D, West JD, Messinger SM, Mott KA. Evidence for complex collective dynamics and emergent distributed computation in plants. Proc Natl Acad Sci USA 2004; 1001:918-22.
41. Van der Putten WH, Vet LEM, Harvey JA, Wackers FL. Linking above and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. Trends Ecol Evol 2001; 16:547-54.
42. Mithöfer A, Wanner G, Boland W. Effects of feeding *Spodoptera littoralis* on lima bean leaves. II. Continuous mechanical wounding resembling insect feeding is sufficient to elicit herbivory related volatile emission. Plant Physiol 2005; 137:1160-8.
43. Pearce G, Ryan CA. Systemic signaling in tomato plants for defense against herbivores: isolation and characterization of three novel defense signaling glycopeptide hormones coded in a single precursor gene. J Biol Chem 2003; 278:30044-50.
44. Zipfel C, Felix G. Plants and animals: a different taste for microbes? Curr Opin Plant Biol 2005; 8:353-60.
45. Nomura K, Melotto M, He SY. Suppression of host defense in compatible plant Pseudomonas syringae interactions. Curr Opin Plant Biol 2005; 8:361-8.
46. Walker TS, Bais HP, Grotewold E, Vivanco JM. Root exudation and rhizosphere biology. Plant Physiol 2003; 132:44-51.
47. Romero GQ, Benson WW. Biotic interactions of mites, plants and leaf domatia. Curr Opin Plant Biol 2005; 8:436-40.
48. Callaway RM. The detection of neighbors by plants. Trends Ecol Evol 2002; 17:104-5.
49. Dessaux Y. Biological communications and interactions in the rhizosphere. Presented at "Rhizosphere 2004" congress, 12. 17. September 2004, Munich/Germany.
50. Dunn AK, Handelsman J. Toward an understanding of microbial communities through analysis of communication networks. Antonie van Leeuwenhoek 2002; 81:565-74.
51. Teplitski M, Robinson JB, Bauer WD. Plants secrete substances that mimic bacterial N acyl homoserine lactone signal activities and affect population density dependent behaviors in associated bacteria. Mol Plant Microbe Interact 2000; 13:637-48.
52. Federle MJ, Bassler BL. Interspecies communication in bacteria. J Clin Investig 2003; 112:1291-9.
53. Hirsch AM, Bauer WD, Bird DM, Cullimore J, Tyler B, Yoder JI. Molecular signals and receptors: controlling rhizosphere interacting between plants and other organisms. Ecology 2003; 84:858-68.
54. Sharma A, Ahgal M, Johri BN. Microbial communication in the rhizosphere: Operation of quorum sensing. Curr Sci 2003; 85:1164-72.
55. Jorgensen R. The origin of land plants: a union of alga and fungus advanced by flavenoids. BioSystems 1993; 31:193-207.
56. Zyalalov AA. Water flows in higher plants: physiology, evolution and system analysis. Russian J Plant Physiol 2004; 51:547-55.
57. Jorgensen RA. Restructuring the genome in response to adaptive challenge: McClintock's bold conjecture revisited. Cold Spring Harbor Symposia on Quantitative Biology 2004; 69:349-54.
58. Denison RF, Kiers TE. Why are most rhizobia beneficial to their plants, rather than parasitic? Microbes Infect 2004; 6:1235-9.
59. Vandenkoornhuyse P, Baldauf SL, Leyval C, Straczek J, Young JP. Extensive fungal diversity in plant roots. Science 2002; 295:2051.
60. Estabrook EM, Yoder JI. Plant plant communications: rhizosphere signalling between parasitic angiosperms and their hosts. Plant Physiol 1998; 116:1-7.
61. Yoder, JI. Parasitic plant responses to host plant signals: a model for subterranean plant plant interactions. Curr Opin Plant Biol 1999; 2:65-70.
62. Keyes WJ, O'Malley RC, Kim D, Lynn DG. Signaling organogenesis in parasitic angiosperms: xenognosin generation, perception and response. J Plant Growth Regul 2000; 19:217-31.
63. Kahmann R, Basse C. Fungal gene expression during pathogenesis related development and host plant colonization. Curr Opin Microbiol 2001; 4:374-80.
64. Imaizumi Anraku H, Takeda N, Cherpentier M, Perry J, Miwa H, Umehara Y, Kouchi H, Murakami Y, Mulder L, Vickers K, Pike J, Downie A, Wang T, Sato S, Asamizu E, Tabata S, Yoshikawa M, Murooka Y, Wu GJ, Kawaguchi M, Kawasaki S, Parniske M, Hayashi M. Plastid proteins crucial for symbiotic fungal and bacterial entry into plant roots. Nature 2005; 433:527-31.
65. Van West P, Morris BM, Reid B, Appiah AA, Osborne MC, Campbell TA, Shepherd SJ, Gow NAR. Oomycete plant pathogens use electric fields to target roots. Mol Plant Microbe Interact 2002; 15:790-8.
66. Samaj J, Baluska F, Voigt B, Schlicht M, Volkmann D, Menzel D. Endocytosis, actin cytoskeleton and signaling. Plant Physiol 2004; 135:1150-61.
67. Guerts R, Fedorova E, Bisseling T. Nod factor signaling genes and their function in the early stages of Rhizobium infection. Curr Opin Plant Biol 2005; 8:346-52.
68. Lammers PJ. Symbiotic signaling: new functions for familiar proteins. New Phytol 2004; 161:324-6.
69. Brundrett MC. Coevolution of roots and mycorrhizas of land plants. New Phytol 2002; 154:275-304.
70. Müller CB, Kraus J. Symbiosis between grasses and asexual fungal endophytes. Curr Opin Plant Biol 2005; 8:450-6.
71. Schultz JC, Appel HM. Cross kingdom cross talk: hormones shared by plants and their insect herbivores. Ecology 2004; 85:70-7.
72. Roossinck MJ. Symbiosis versus competition in plant virus evolution. Nat Rev Microbiol 2005; 3:917-24.
73. Shackelton LA, Holmes EC. The evolution of large DNA viruses: combining genomic information of viruses and their hosts. Trends Microbiol 2004; 12:458-65.
74. Dunoyer P, Voinnet O. The complex interplay between plant viruses and host RNA silencing pathways. Curr Opin Plant Biol 2005; 8:415-23.
75. Wang MB, Metzlaff M. RNA silencing and antiviral defense in plants. Curr Opin Plant Biol 2005; 8:216-22.
76. Dunnoyer P, Voinnet O. RNA as a signalling molecule. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:49-83.
77. Turkington, R, Sackville Hamilton, R, Gliddon C. Within population variation in localized and integrated responses of *Trifolium repens* to biotically patchy environments. Oecologia 1991; 86:183-92.

78. Tomilov AA, Tomilova NB, Abdallah I, Yoder JI. Localized hormone fluxes and early haustorium development in the hemiparasitic plant *Triphysaria versicolor*. Plant Physiol 2005; 138:1469-80.
79. Press MC, Phoenix GK. Impacts of parasitic plants on natural communities. New Phytol 2005; 166:737-51.
80. La Cerra P, Bingham R. The Origin of Minds. New York: Harmony Books, 2002.
81. Xoconostle Cázares B, Xiang Y, Ruiz Medrano R, Wang HI, Monzer J, Yoo BC, McFarland KC, Franceschi VR, Lucas WJ. Plant paralog to viral movement protein that potentiates transport of mRNA into the phloem. Science 1999; 283:94-8.
82. Baluska F, Volkmann D, Barlow P. Eukaryotic cells and their cell bodies: cell theory revised. Ann Botany 2004; 94:9-32.
83. Gillespie T, Oparka KJ. Plasmodesmata—gateways for intercellular communication in plants. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:109-46.
84. Golz JF. Lessons from the vegetative shoot apex. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:147-77.
85. Srinivas BP, Hülskamp M. Lessons from leaf epidermal patterning in plants. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:225-39.
86. Tassetto M, Maizel A, Osorio J, Joliot A. Plant and animal homeodomains use convergent mechanisms for intercellular transfer. EMBO Rep 2005; 6:885-90.
87. Kim I, Zambryski PC. Cell to cell communication via plasmodesmata during Arabidopsis embryogenesis. Curr Opin Plant Biol 2005; 8:593-9.
88. Kurata T, Okada K, Wada T. Intercellular movement of transcription factors. Curr Opin Plant Biol 2005; 8:619-24.
89. Bonke M, Tähtiharju S, Helariutta Y. Lessons from the root apex. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:199-223.
90. Schilmiller AL, Howe GA. Systemic signaling in the wound response. Curr Opin Plant Biol 2005; 8:369-77.
91. McClintock B. The significance of responses of the genome to challenge. Science 1984; 226:792-801.
92. Goh CH, Nam HG, Park YS. Stress memory in plants: a negative regulation of stomatal response and transient induction of rd22 gene to light in abscisic acid entrained Arabidopsis plants. Plant J 2003; 36:240-55.
93. Trewavas A. Aspects of plant intelligence. Ann Bot 2003; 92:1-20.
94. Coupland G. Intercellular communication during floral initiation and development. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:178-97.
95. McCubbin AG. Lessons in signalling in plant self incompatibility systems. In: Fleming AJ. ed. Intercellular Communication in Plants. Annual Plant Reviews. Oxford: Blackwell Publishing 2005; 16:240-75.
96. Baluska F, Volkmann D, Barlow PW. Cell-cell channels and their implications for cell theory. In: Baluska F, Volkmann D, Barlow PW. eds. Cell-cell channels. Eurekah.com 2005; 1-17.
97. Bell, P. Viral eukaryogenesis: was the ancestor of the nucleus a complex DNA virus? J Mol Ev 2001; 53:251-6.
98. Ryan, F. Darwin's blind spot: evolution beyond natural selection. Boston. Houghton Mifflin Company, 2002.
99. Villarreal, LP. Viruses and the Evolution of Life. Washington, D.C.: ASM Press, 2005.
100. Thompson KR, Olofsdotter OK, Chen DY, Zhao Y, O'Dell TJ, Martin KC. Signaling from synapse to nucleus during long term synaptic plasticity: a role for the classical active nuclear import pathway. Neuron 2004; 44:997-1009.
101. Martin KC. Local protein synthesis during axon guidance and synaptic plasticity. Curr Opin Neurobiol 2004; 14:305-10.
102. Moccia R, Chen D, Lyles V, Kapuya EEY, Kalachikov S, Spahn CMT, Frank J, Kandel ER, Barad M, Martin KC. An unbiased cDNA library prepared from isolated Aplysia sensory neuron processes is enriched for cytoskeletal and translational mRNAs. J Neurosci 2003; 23:9409-17.
103. Andersson JO. Lateral gene transfer in eukaryotes. Cell Mol Life Sci 2005; 62:1182-97.
104. Meagher TR, Vassiliadis C. Phenotypic impacts of repetitive DNA in flowering plants. New Phytol 2005; 168:71-80.
105. Strand A. Plastid to nucleus signalling. Curr Opin Plant Biol 2004; 7:621-5.
106. Dugas DV, Bartel B. MicroRNA regulation of gene expression in plants. Curr Opin Plant Biol 2004; 7:512-20.
107. Bender J. Chromatin based silencing mechanisms. Curr Opin Plant Biol 2004; 7:521-6.
108. Jablonka E, Lamb MJ. The changing concept of epigenetics. Ann N Y Acad Sci 2002; 981:82-96.
109. Rapp RA, Wendel JF. Epigenetics and plant evolution. New Phytol 2005; 168:81-91.
110. Kumar A, Bennetzen JL. Plant retrotransposons. Annu Rev Genet 1999; 33:479-532.
111. Kovalchuk I, Kovalchuk O, Kalck V, Boyko V, Filkovski J, Heinlein M, Hohn B. Pathogen induced systemic plant signal triggers DNA rearrangements. Nature 2003; 423:760-2.
112. Samaj J, Read ND, Volkmann D, Menzel D, Baluska F. The endocytic network in plants. Trends Cell Biol 2005; 15:425-33.
113. Lolle SJ, Victor JL, Young JM, Pruitt RE. Genome wide non mendelian inheritance of extra genomic information in Arabidopsis. Nature 2005; 434:505-9.
114. Weigl D, Jürgens G. Genetics. Hotheaded healer. Nature 2005; 434:443.
115. Pearson H. Cress overturns textbook genetics. Nature 2005; 434:351-60.
116. Witzany G. Natural history of life: history of communication logics and dynamics. S.E.E.D. Journal 2005; 5:27-55.